Online adjustments in goal-directed movements during ageing

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2020

Chapter 7

General discussion

This thesis contributes to a better understanding of the online adjustments during ongoing movements in upper and lower limbs and the differences between young and older adults. The main results show that adults of all ages can adjust their movements fast, whichever in reaching or stepping task, perturbed by whichever types of stimuli. The underlying online control of the online adjustments may be similar.

Summary on the research questions, hypotheses and answers of each study:

Chapter	Questions	Hypotheses	Answers
2	Are fast adjustments of the arm are accompanied by postural adjustments?	Yes.	Yes.
	Is the manual following response similar to the response to a target jump?	Yes.	Yes, but head responses are different.
4	Is the manual following response a compensation of apparent self-motion?	Yes.	No.
5	Are muscle adjustments and foot adjustments well below 200 ms?	Yes.	Yes.
3	How do older adults respond to visual perturbations compared to young ones in reaching?	Reduced and later responses.	Yes to target jump (larger to background motion).
6	How do older adults respond to target jumps compared to young ones in walking?	Reduced and later responses.	Yes in behaviour, not much in EMG.

Control of posture while reaching towards the target

In the tasks that were under study in this thesis, reaching a target with either hand or foot was always the goal of the tasks. However there was an additional hidden goal: keeping balance. There are interactions between those two task requirements: balance is challenged by moving the arm, while the accuracy of the goal-directed arm movement is challenged by maintaining balance (Berrigan et al. 2006). Obviously, reaching while standing (Chapters 2-4) makes the goal-directed task more challenging compared to reaching with the arm from a sitting position. Similarly, stepping while walking (Chapters 5 and 6) makes it more difficult compared to leg reaching during quiet stance.

When balance maintenance is more demanding, one needs anticipatory postural adjustments (APA). Despite the earlier postural responses, manual responses are still fast, and those adjustments in response to perturbations include other postural changes apart from the reaching hand (Fautrelle et al., 2010). In the present thesis, the results show that due to perturbations postural responses do occur earlier than responses in the moving hand or foot. For example, during arm reaching, the adjustment of the upper trunk has shorter latency than that of the hand (~70 ms vs. ~110 ms, Chapter 2); additionally, during stepping, fast responses show up in both legs (EMG: ~120 ms, Chapter 5).

In reaching, the upper trunk response can be regarded as a part of anticipatory postural adjustments (APA, Chapters 2, 3). However, in walking the stance-leg responses may not be classified as APA (Chapters 5, 6) for two reasons. First, the early-responding muscles adjusted at about the same time for both legs, so the response of the contralateral leg could not be a part of an APA. Second, the fact that the centre of pressure (COP) response that started before the kinematic response of the swing foot is not evidence for an anticipatory response either. This difference in response latency is likely to be due to differences in the profile's sensitivity for latency determination (a higher derivative component of COP lead to an earlier latency), as discussed in Chapter 5.

Online control process

All the various perturbations used in the present thesis triggered the online adjustments. Those corrective responses in different tasks were all fast (young adults: 70-125 ms), which suggested similar online control processes, namely via feedforward estimation and feedback correction, whatever the pathway to process sensory information and motor signals are specific to the type of perturbation assessed. Even though some latency differences exist for various perturbation types which might reflect differences in the pathway involved or the information processing level as will be discussed below.

Comparison of target jump and background motion (Chapter 2)

The responses to target jumps and background motion were similar in latency (~120 ms) and the responses were both in the direction of the perturbation. An important difference was that the target jump did not induce the head response, whereas the background motion did. This might be due to a misjudgement of the target position, or due to apparent self-motion such that the head compensated for it. As the compensation for self-motion was rejected (see further), an alternative explanation might be a 'binding' error. In other words, different properties across separate areas of the visual cortex might be bound when they were relevant for the task at hand (Treisman, 1996). Therefore, sudden background motion was detected near the target and the brain might attribute this motion to the location of the target. Motion of obstacles near the target could also trigger similar manual responses (Aivar et al., 2008).

Comparison of Background motion and galvanic vestibular stimulation (GVS, Chapter 4)

It was hypothesised that both background motion and GVS would induce inferred self-motion (as noticeable in the head response), and that the hand would responded as well to compensate for that. However, the results showed that the background motion induced a much larger hand response than GVS did, with similar head responses (evidence for inferred self-motion). Therefore, the hypothesis was rejected.

Regardless of the origin of sensory information, the adjustments are fast, and are still within the time window of the response latency of fast online control (around 100 ms to well below 200 ms). A shorter response latency induced by GVS compared to background motion (~80 ms vs. ~125 ms) is logical because vestibular neuronal delays are shorter than visual delays.

Comparison of adjustments of the upper limb and the lower limb (Chapter 2 with 5, Chapter 3 with 6)

In young adults, the response latency for the upper limb was 110-125 ms (older: 125-140 ms) and for the lower limb was 155 ms (older: 180 ms). At the behavioural level, the foot adjustments started about 30-55 ms later than the hand adjustments. This delay of several tens of milliseconds for the lower limb may be partly due to longer transmission distance to the muscles, and also possibly due to more demanding balance maintenance. The latter is evidenced in a study of Reynolds and Day (2005) showing that gait initiation without weight support could increase the latency by 0-8 ms. At the EMG level, the limb muscle could respond around 40 ms earlier than the kinematics of distal end of the limb, both in reaching (Fautrelle et al., 2010) and stepping (Chapter 5).

It is still not certain which pathway is responsible for fast online adjustments. Some have argued that the pathway involved is subcortical. This is suggested to be mediated by visual inputs via reticulospinal pathway through superior colliculus, and argued since the latencies were the same regardless of the target displacement direction and hand side (Day and Brown, 2001). In a monkey study, neurons in superior colliculus can relay and transmit limb movement information to the spinal motor system (Werner et al., 1997). Others have argued that online adjustments are mediated via a cortical pathway. Posterior parietal cortex (PPC) seems to be involved in fast online adjustments (Desmurget et al., 1999; Pisella et al., 2000; Reichenbach et al., 2011), possibly by visual feedback processing (Wenderoth et al., 2006), and the anterior part of parietal cortex seems to be involved in proprioceptive feedback processing (Filimon et al., 2009). In addition, it is argued that the cerebellum is involved in the state estimation (Shadmehr and Krakauer, 2008), which is certainly a part in the online control process, and underscored by cerebellar lesions found to influence fast corrections (Hoogkamer et al., 2017). Gomi et al. (2008) put up a model of multilevel control that low-level visuomotor control interacts with higher control, related to the computational load and automaticity. To summarise, it seems that the pathways used in online control depend on the complexity of the sensory feedback and the level to process information.

Effects of ageing

The results of the studies comparing the online adjustments in young and older adults revealed several interesting findings.

First, the older adults could perform the task as accurately as the young however they used more time to reach the target. When the whole movement takes longer time for a certain distance, the vigour (in acceleration) becomes less. In the reaching task, the older adults showed longer movement time and less vigour (Chapter 3). As a result, they could perform as accurate as the young adults at the endpoint. In the walking task, the treadmill speed and distance between stepping-targets were fixed so both age groups had similar movement time (swing duration) and similar vigour (Chapter 6). However, this was at a cost of endpoint error for the older adults, and later response also made their correction less complete. Interestingly, for medial adjustments, young and older adults had similar correction (Chapter 6). This similarity could be due to the balance constraints for both age groups.

Secondly, how the weight given to sensory information changes with age depends on the task and stimuli. Previous studies have shown that older adults rely on vision more to control posture (Jamet et al., 2004; Poulain and Giraudet, 2008), and are less good at ignoring irrelevant background motion than young adults (de Dieuleveult et al., 2017). These evidences support the results in this thesis that the older adults relied more on background motion compared to the young. The weight of sensory information was task-dependent as when the task was to maintain balance on a moving platform, older adults rely greatly on proprioceptive information (Wiesmeier et al., 2015). In Chapter 3, the elderly responded more strongly to the surrounding motion (large area) in goal-directed movements, supporting our interpretation of this response in terms of binding information rather than apparent self-motion.

Thirdly, the response latency in the elderly has similar prolongation (around 20 ms) at the behavioural level for the upper limb (Chapter 3) and lower limb (Chapter 6). This was thus regardless of whether they took more time to execute a movement or were less accurate in reaching the target. This increase of response latency is in line with what has been found by others in reaching (Kadota and Gomi, 2010; Kimura et al., 2015). So, the prolongation in response latency for older adults exists, though the exact value can be affected by the set-up, stimuli, and the method of determining the latency. The general slowing may play an important role in this prolongation, in which all factors related to force-impulse control could be involved (Clark et al., 2011). As what has been found in walking (Chapter 6), the EMG delay (below 10 ms) was not as much as the behavioural delay (~20 ms). This suggests a deficit in muscle force development for the older adults, which also makes muscle training promising to improve their ability to make online adjustments. Therefore, it is promising to achieve 'healthy ageing' by an active lifestyle to maintain muscle functions.

Future direction

The present thesis did elucidate various aspects of the online movement adjustments in upper and lower limb movements, however several questions remain to be answered and addressed in future work.

The perturbation timing plays an important role to induce fast online adjustments. Different time pressure is evaluated in reaching (Chapter 3) and walking (Chapters 5, 6). Future research can focus on the effects of time pressure on the responses, especially on the response latency.

Besides general muscle training, the time pressure could be introduced into the training program. For example, in the paradigm of stepping-target shifts during walking, older adults may also be trained to successfully adjust to target shifts, by levering up the time pressure. In addition, the distance of target shift can also be individualised to better fit each participant's walking pattern, and encourage them to make more attempts. Clinically, it is promising to use the training paradigm to benefit older adults with high risk of falls.

Lastly, the pathways of online adjustments still need to be understood. The usage of transcranial magnetic stimulation (TMS) or electroencephalogram (EEG) may provide more insights to the brain structures that contribute to online adjustments.

Conclusion

Adjusting an on-going goal-directed movement can be fast within 160 ms. The limb and other body parts all contribute to the online adjustments. The upper limb and lower limb may be controlled in a similar way when approaching a goal. Moreover, those online adjustments are delayed and decreased during ageing, mostly because of deteriorated muscle functions.